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The pros and cons of applying the movement ecology paradigm for studying animal dispersal

Michel Baguette[1,2*], Virginie M Stevens[1] and Jean Clobert[1]

Abstract

Understanding how dispersal movements are motivated and executed is the core business of dispersal evolutionary ecology, which is an active research field in environmental sciences. However, recent advances in dispersal research have not yet been confronted to the movement ecology paradigm (MEP) that was introduced to unify the study of all types of movements of all organisms. Here we aim at doing this exercise to investigate if the MEP is sufficiently general to provide sound predictions on dispersal causes, modalities and consequences. We begin by briefly summarizing the main concepts of the MEP that are relevant to our analysis. A part of some examples, many studies focusing on animal movements share a common, two step procedures: (1) record movement paths, and (2) test post-hoc functional assumptions to identify the relationships between the four basic components listed above. Then we present some important results from dispersal evolutionary ecology research. Next we turn to two groups of model organisms (butterflies and lizards), in which dispersal has been thoroughly studied in the field for decades. These organisms have contrasted dispersal modes: the causes of dispersal are mainly related to the social context in lizards, whereas they are mainly dependent on the environmental context in butterflies. Lizards disperse most often once in their life soon after birth, whereas butterflies generally disperse all over their adult life. We investigate if and how the MEP provides an added value to the study of dispersal on these organisms. Although the MEP is in principle encapsulates almost every variation acting on movement, its ability to incorporate variation in anything else than pure movement trajectories appears to be mixed: dispersal is extremely phenotype- and context-dependent, which rends difficult the use of the MEP as an operational tool to incorporate variation across individuals and situations. We propose that a mixed approach combining the Eulerian and Lagrangian viewpoints could deal with this high dispersal variability. We conclude by providing perspectives for the integration of ecological and evolutionary processes affecting dispersal into the MEP that could increase its efficiency to study dispersal.

Keywords: Dispersal syndrome, Eulerian approach, Lagrangian approach, Metapopulation, Landscape genetics, Kin competition, Inbreeding, Lifetime movement effort, Energetics, Genomics

Introduction

Dispersal, movements potentially leading to gene flow [1], is inherently associated with changes of location of gametes, zygotes or individuals. Understanding how these movements are motivated and executed is the core business of dispersal evolutionary ecology, which is an active research field in environmental sciences [2,3]. Recent advances in dispersal research indeed document that dispersal is a multi-causal process [4] under strong selective pressures [5]. Accordingly, dispersal shows strong intra-specific variation [6] that is associated with other key life history traits to shape real dispersal syndromes; that is, patterns of covariation of morphological, physiological, behavioral and life history traits are important and prevalent [7,8]. These syndromes have consequences on both (meta)-population spatial dynamics [9] and dispersal evolution [10] that are crucial in the current era of climate change [11] and habitat fragmentation [12,13]. However, this solid dispersal evolutionary ecology framework has not yet been confronted to the movement ecology paradigm (MEP) that was introduced to unify the study of all types of movements of all organisms [14]. Here we aim at doing this exercise to investigate if the MEP is sufficiently general to provide sound predictions on dispersal causes, modalities

* Correspondence: baguette@mnhn.fr
[1]CNRS USR 2936, Station d'Ecologie Expérimentale du CNRS, route du CNRS, F-09200 Moulis, France
[2]Muséum National d'Histoire Naturelle, Institut de Systématique, Evolution et Biodiversité, UMR 7205, 57 rue Cuvier, F-75005 Paris cedex 5, France

and consequences. We will begin by briefly summarizing the main concepts of the MEP that are relevant to our analysis. Then we will selectively review some appropriate outcomes of dispersal evolutionary ecology. Next we will turn to selected model organisms, in which we will investigate if and how the MEP provides an added value to the study of dispersal. We will conclude by providing a roadmap for further research that could increase the efficiency of the MEP in the study of dispersal.

Review

The MEP in a nutshell

To facilitate integration among movement types and organisms, the MEP advocates a mechanistic approach applicable to all types of movement. Nathan et al. [14] proposed that movement paths are actually the outcome of the interaction between four basic components: the motion capacity, the navigation capacity, the internal state of the individual and the external state of the environment (Figure 1). The motion capacity is the suite of traits that enables the individual to move. The navigation capacity is the suite of traits that enables the individual to orient its movement in space and/or time. The internal state encompasses all factors specific to the individual that will affect its propensity to move. The external state combines all social and environmental factors that affect the movement of the individual. Movement paths produced by the interaction between these four components are elementary units that can be further classified according to their functionality during the life of the individual [14,15]. The sum of movements realized by an individual over its life (its lifetime track: [16]) can then be disentangled according to the functionality of successive elementary units, and related to social and environmental factors. Most studies based on the MEP share thus a common, two step procedure: (1) record movement paths, and (2) test post-hoc functional assumptions to identify the relationships between the four basic components listed above (e.g. [17-19]). The precision of the description of the movement paths is an essential prerequisite to the first step. Nathan et al. [14] rightly insist on the current development of remote sensing recorders and the simultaneous availability of powerful computers allowing the fast treatment of huge data sets. These technical advances will obviously facilitate the simulation of the movements of virtual individuals, and the comparison of simulated trajectories to real, observed paths, which is a self-declared goal of the MEP [15]. The identification of coherent algorithms that correctly echo real individual movements is a solid advantage that allows testing scenarios including variation in the relative influence of the four basic components, which ultimately provides a way to identify the functionality of different movement paths according to the social (e.g. [20]) or environmental (e.g. [21,22]) contexts.

Dispersal evolutionary ecology

The net result of dispersal is gene flow [1]. This can be achieved by multiple ways, as any mechanisms that affect the physical location of an organism can eventually contribute to dispersal [4]. Dispersal associates space and time use in contrasted strategies, with the emergence of dissimilar lifestyles. In sedentary organisms, movements leading to gene flow occur rarely in the life of an individual, whereas nomadic organisms may exhibit extremely long lifetime tracks and disperse their genes throughout [23]. Given such huge differences among organisms,

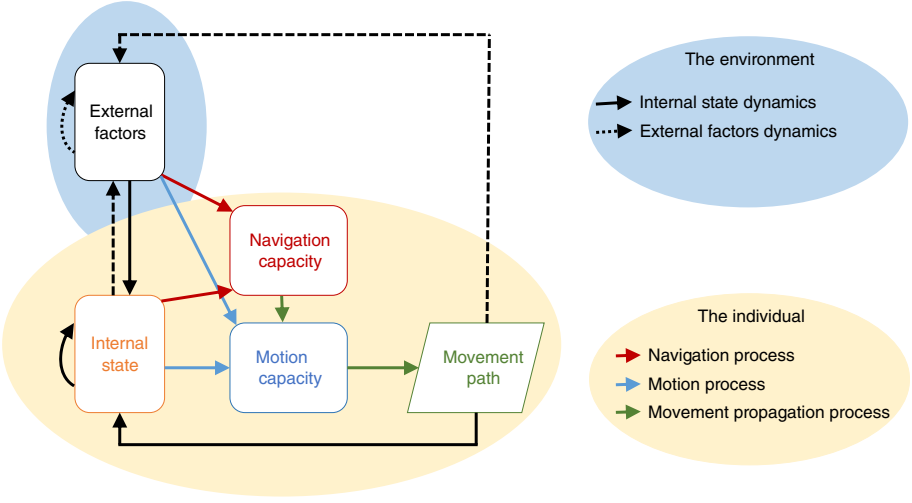

Figure 1 The movement ecology paradigm. Movement paths are the outcome of four inter-related components. Three components (internal state, motion capacity, navigation capacity) are related to the individual (yellowish background), whereas the fourth one is related to the environment (bluish background). Arrows symbolize the relationships among these four components. Redrawn from Nathan et al. [66].

dispersal remains a rather elusive process (e.g. [3,24]). However, there are several characteristics that distinguish dispersal from other types of movements (foraging, migration), which occur in most, if not all living organisms. Causes of dispersal are the most prominent among these general characteristics [2,4,25-27]). Dispersal is indeed a general solution to three different, not necessarily interrelated, problems. First, dispersal resolves social conflicts, by preventing kin competition and limiting intra-specific competition. Second, dispersal limits the mating among relatives, and hence decreases the fitness erosion associated with the "inbreeding kiss of death" [28]. Finally, dispersal provides a means for exploiting newly favorable abiotic and biotic conditions. These three main causes of dispersal entail the evolution of condition-dependent dispersal strategies. A recent review provides an exhaustive synthesis of all the existing models of dispersal evolution [27]. We decided thus to walk here on the empiricist side and to complement this theoretical exercise by selected examples drawn from real organisms. In experimental conditions, common lizards exposed to kin competition dispersed in more risky conditions than those being confronted to the competition with non kin individuals [29,30]. In the two spotted mite, relatedness, but not density, changes the shape of the dispersal kernel towards a more skewed and leptokurtic shape including a longer dispersal distance when kin competition occurs [31]. Such results indicate that both the decision to disperse and the distance of dispersal are conditional to kin competition, or put in the MEP terminology, competition with kin (an external factor) affects the propensity to disperse (internal state), yielding longer dispersal distances (movement path). Recent evidence in a social bird also showed that inbreeding avoidance might act on dispersal distance, individuals dispersing twice as farther from natal groups than from non-natal groups [32]. However, dispersal is not the only route to avoid inbreeding in that bird species, an alternative would be to retain from dispersing, and to mate with a distant relative within the natal group, which is the only way to attain a breeding position [32]. Thus here again not only the decision to disperse, but also the distance of dispersal is conditional to inbreeding avoidance. Changes in dispersal according to environmental quality were documented in a butterfly where experimental changes of habitat quality steeply modified dispersal rates within a metapopulation. Habitat quality was experimentally decreased in low quality patches, while high quality patches remained unchanged. The probability that an individual would leave treated patches increased, whereas it decreased from untreated patches. Individual dispersal decision, a change in the internal state of the individual, was thus here conditionally dependent on the quality of the habitat [33].

Beyond the evidence of such conditional strategies, a strong recent advance in dispersal evolutionary ecology is the demonstration that dispersal is phenotype-dependent (e.g. [26]). There is often a large, non-random intra-specific variability in dispersal, even in homotypic species with no discrete morphological differences between individuals with different dispersal phenotypes (e.g. [6,34]). But individuals with different dispersal phenotypes also differ in suite of traits (e.g. size, physiology or behavior), which means that different dispersal strategies are associated with, and even shape, different life-histories between as well as within than between species [7,8,35,36]. For instance, it has been suggested that the personality of individuals, that is, how they react to various stimuli, is a crucial factor in determining dispersal decision and distance. Cote et al. [30] present a verbal model in which they propose that asocial, bold, aggressive and fast exploring individuals will be mainly long-distance colonizers, whereas more social, shy and slow explorer individuals will be those that join existing populations. These predictions were confirmed by empirical observations on an invasive fish [37]. Given the existence of such trade-offs, we thus expect that individuals with different dispersal strategies will have contrasted fitness expectations in the same metapopulation. If different dispersal phenotypes have differences in fitness expectation in a particular landscape, it will directly influence the distribution of individuals in a metapopulation, which will hence affect their movement paths. Considering the large inter-individual variation in dispersal and life-histories within species, we expect thus inter-individual differences in the answer to the same environmental problem. How such differences will in turn impact population dynamics is a key question with potentially strong consequences. Although the MEP is not ignoring it, the incorporation of such consequences on population dynamics cannot be easily handled in the MEP framework.

Dispersal is indeed a central ingredient of metapopulation spatial dynamics, by allowing the (re)colonization of empty habitat patches, or the rescue of declining population (e.g. [9,38]). But metapopulation spatial dynamics in turn influence the evolution of dispersal, by (counter-) selecting particular dispersal phenotypes according to the state of the metapopulation (e.g. [30]). This is particularly obvious in positive or negative-density dependent dispersal where dispersal decision at the individual level is triggered according to the state of the local population (kinship, density of conspecifics, sex-ratio). Therefore, the density threshold at which dispersal decision will happen is a key target for dispersal evolution, which depends on the cost-benefit balance of dispersal in each metapopulation. For instance, Simmons & Thomas [39] reported that bush cricket density threshold inducing the ontogeny of long-winged individuals dispersing over long distance was lower in populations at expanding range

margins. Beside density, the cost-benefit balance of dispersal depends also on habitat quality and on the social and genetic structures of local populations. Variation in these parameters will entail uncertainty on the cost-benefit balance of dispersal, which should favor the emergence of contrasted dispersal strategies. To sum up, we point out the discrepancy between the ecological focus of the MEP in which the emphasis is on mechanistic understanding of the movement process, whereas many of the dispersal studies are focused on the evolutionary drivers and consequences of dispersal.

Model organisms

We will now turn to two model organisms to investigate if and how the movement ecology paradigm and dispersal evolutionary ecology could be integrated. These two models (butterflies and lizards) have contrasted life-style, which should give some generality to our analysis. For most butterflies, dispersal is mainly constrained by environmental factors, and potentially occurs all over the adult stage. Dispersal is defined by an individual passing from a discrete habitat patch in the landscape into another patch. This leads to the need of a suitable definition of habitat (patch-matrix *vs*. continuum, which are the two extremes of a continuum according to landscape grain, [40]). Butterflies potentially sample their environment all over their adult stage, and maximum dispersal distances can exceed 100 km in some species [34]. For most lizards, dispersal is mainly driven by the social and thermal environment, and occurs once in its life soon after birth. In the common lizard, dispersal is defined by a displacement exceeding 30 m from the individual's mother home range, defined as the upper 95% confidence limit of the home range diameter [41]. Maximum dispersal distances are around 100 m [41]. After dispersal, individuals occupy the same home range all over their life. Differences in dispersal definition between butterflies and lizards (habitat vs. home range) correspond to two dissimilar strategies of space use mentioned before (nomadism vs. sedentary), in which dispersal triggers are generally rather environmental (nomadism) or social (sedentary).

Butterflies

Butterflies have been recognized as ideal models for the study of dispersal (e.g. [34]) because (1) for most species, their specialization makes their habitats relatively easy to map in heterogeneous landscapes (80% of the Holarctic butterfly species live in predominantly-closed population structure: [42]) and (2) the life history of most species is well documented (e.g. [8,43]). Besides, they are easy to manipulate in large numbers, they can be monitored using standard capture-mark-recapture procedures (e.g. [33]) and the scale of their movements is tractable in space and time (e.g. [44-46]). Finally, some species are easy to breed in captivity, paving the way for experimental studies on dispersal [47,48] including selection experiments [49].

Butterfly dispersal is strongly affected by the grain of the landscape, the smallest spatial scale at which an organism recognizes spatial heterogeneity according to its perceptual range, which is the basic limitation of animal perception [40]. A landscape is fine-grained if the density of habitat patches is high, and coarse-grained when the density of habitat patches is low (see Figure 2A for a graphic representation of coarse- and fine-grained landscapes). In the bog fritillary butterfly (*Boloria eunomia*), fine- and coarse-grained landscapes differ in the mortality probability associated to the dispersal process, which is much higher in coarse grained landscapes: 0.05 vs. 0.3 in landscapes with ca. 50% and 0.4% of suitable habitats, respectively (Figure 2) [45]. Unsurprisingly, the three steps of the dispersal process (emigration, transience and immigration) are modified by the grain of the landscape. The probability that a given individual emigrates severely decreased in coarse-grained landscapes respective to fine-grained landscapes (0.4 vs. <0.01) for the bog fritillary butterfly (Figure 2) [45]. This decrease was due to the reluctance of flying individuals to cross habitat edges, which translated into modified movement paths within habitats: there is an increase of the frequency of U-turns at habitat borders in coarse-grained landscapes [44,46]. In the same species, transience movements were of similar topology than foraging movements within the habitat in fine grained landscapes. However, both movements were topologically different in coarse grained landscapes: within habitats, butterflies fly short bouts and turn frequently, and between habitats they fly longer bouts with significantly straighter trajectories [46,50]. The switch from foraging-like dispersal movements in fine-grained landscapes to special dispersal movements in coarse grained landscape is most probably associated to the costs associated to dispersal in the latter situation [45], because straighter movements with longer bouts increased flight speed and thus decreased the time spent in hostile environments [50]. Finally, immigration also appears affected by the landscape grain: in coarse grained landscape, the navigation capacity increased. Merckx & Van Dyck [51] reported a two fold increase in the perceptual range (the distance of detection of the habitat) of individuals of a woodland butterfly (the speckled wood *Pararge aegeria*) from agricultural landscapes with small and sparse woodlots as compared to individuals from deep forests.

Overall, by focusing on movement paths the approach used here to infer how landscape structure affects dispersal is not basically different of the approach advocated by Nathan et al. [14]. However, we want to point out the idiosyncratic nature of dispersal evolution according to selective pressures like those associated with changes in

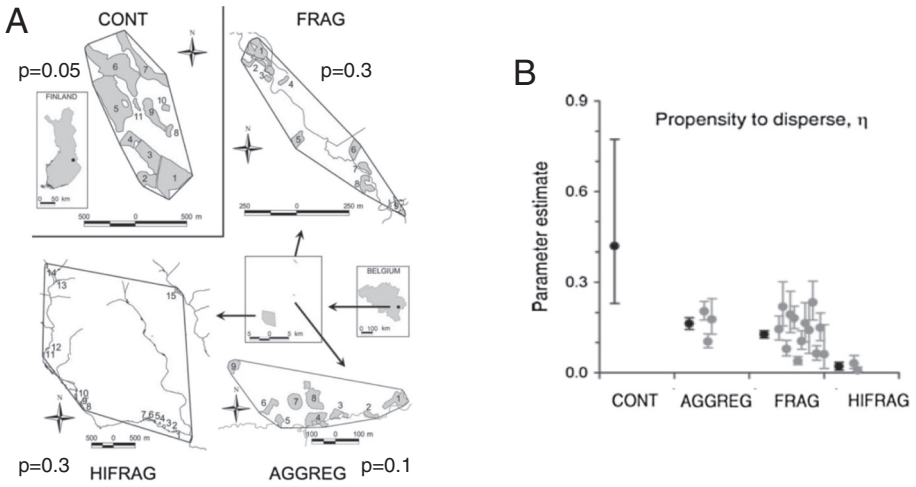

Figure 2 Butterfly dispersal and landscape grain. A. Maps of the four landscapes where dispersal rates among local populations of the bog fritillary butterfly (*Boloria eunomia*) were studied. Landscapes are defined as the minimum convex polygon surrounding local populations. Grey patches symbolize habitats with local populations; the density of the grey patches indicates the grain of the landscape. CONT (continuous): extremely fine-grained landscape, AGREG (aggregated landscape): fine-grained landscape, FRAG (fragmented) landscapes: coarse-grained landscapes; HIFRAG (highly fragmented landscape): extremely coarse-grained landscape. p-values are the probability that a disperser will die during dispersal in each landscape. **B**. Plots of the dispersal propensity, i.e. the probability that an individual will leave a local population in each of the landscapes figured in panel **A**. Black dots and error bars are the mean and the standard error of the parameter averaged over several generations (grey dots and bars). Adapted from Schtickzelle et al. [45].

landscape structure. The variation of the external state of the environment (i.e. passing from a fine- to a coarse-grained landscape) thus strongly modifies (1) the internal state of the individual, by decreasing its dispersal propensity, (2) its motion capacity by increasing flight speed, and (3) its navigation capacity, by increasing its perceptual range. We acknowledge that the MEP emphasized application for a focal single individual, hence was designed to capture within-population variation by examining how the relationships between its four basic components, and the resulting movement path, vary among individuals. However, given that movement evolution is not at the heart of the MEP, there is a risk that movement rules obtained in one landscape will be transferred to another without control or alteration. This means that upscaling a mechanistic model of movements obtained in a fine-grained landscape to a coarse-grained landscape (or vice-versa) could lead to severe biases in the estimate of dispersal events and hence flawed predictions of metapopulation dynamics.

We reported so far on the changes in dispersal strategies observed among populations in different environmental contexts. Butterfly studies provide also the opportunity to investigate individual differences in dispersal strategies. Like other insects, some butterfly species perform yearly movements at the scale of subcontinents. This pattern is quite consistent across several species in the Holarctic, with individuals leaving low latitude areas in spring by heading northwards after emergence. During this flight, they flew continuously, weather permitting, at constant speed and latitude, without being disturbed by the presence of conspecifics. After several days of such flights they mate and females lay eggs. A new generation of adults emerges a few weeks later, and the process restarts. Doing this, adults progressively reaches in summer the northern range of the distribution of the species, where overwintering is impossible due to cold conditions. They breed there, and the adult offspring emerging in fall in this area will head southwards. The whole process corresponds thus to two travelling waves of individuals, moving through the subcontinent north in spring and south in fall, punctuated by successive breeding events. This particular movement pattern has been classically referred in the literature to as migration (e.g. [52]), but it corresponds in fact to our definition of dispersal because it entails gene flow, here at very large geographic scale. Different rationales have been proposed to explain the evolution of these particular dispersal movements, among them the most frequent are the unsuitability of environmental conditions in low latitude areas in summer due to heat, or a heavy parasitic pressures in the southern populations. We suggest that this strategy might evolve as a means to exploiting suitable biotic and/or abiotic habitats.

In the large white butterfly *Pieris brassicae*, a species which perform such long distance dispersal movements in Europe, it was recently shown the existence of a real dispersal syndrome, i.e. patterns of covariation of morphological, physiological, behavioral and life history traits [7,8]. In natural populations in the southern range of the distribution area of the species, the distribution of individual flight performance is clearly bimodal. Flight performance is

associated with other behavioral traits like boldness or exploration, best flight performers being bolder and more explorative [53], and having higher consistency in flight direction after adult emergence [54]. Dispersal events in the metatron, an experimental setting designed to study experimental metapopulations, were also performed significantly more often by the best flight performers [47]. It is assumed that populations in the southern range of the distribution area of the species are composed of individuals showing two co-existing dispersal phenotypes, residents with adults that reproduce near their location of emergence and dispersers with adults undertaking the long distance dispersal movements mentioned above. This assumption is supported by the observation that in summer the frequency of individuals with high flight performance significantly increases in populations of increasing latitudes, which is coherent with a recolonization of northern areas by the disperser phenotype [55]. The long term maintenance of this polymorphism seems to depend on the assortative mating of adults with similar flight performance. Indeed, in experimental conditions, we reported fitness advantages for those pairs in which partners have contrasted wing length. This disassortative mating based on wing length translates into positive assortative mating between individuals with similar flight performances. The coexistence of these two dispersal phenotypes is the most parsimonious explanation of the existence of two genetically determined local adaptations in this long haul dispersing species. The flight direction taken at emergence by dispersing individuals is indeed adapted to minimize the risks of being lost in sea or to be forced to flight over high mountains [56,57]. Besides, adult individuals from Mediterranean areas undertake aestivation to cope with high temperature in summer, which is not the case elsewhere [58,59].

How can the MEP deals with such a complex situation? The four basic components of the MEP (the internal state of the individual, its navigation capacity, its motion capacity and the external state of the environment) clearly differ between individuals according to their dispersal phenotypes. An upscaling of a mechanistic model of movements obtained on one dispersal phenotype to the other (or using a mean phenotype) would lead to severe biases in the estimate of dispersal, either by severely under-estimating long distance dispersal and the long distance colonization of suitable habitats, or by blurring the possibility that local adaptations can emerge. Only studies based on the dispersal evolutionary ecology framework, will be able to capture such differences (experimentally and theoretically driven research).

Lizards

In lizards, the movement ecology is not particularly well known. Some data exist on the colonizing rate of introduced populations [60], and dispersal has been described in only a handful number of species. For these species, data are mainly available on the emigration and immigration phase while almost nothing is known on the transience phase. Nevertheless, lizards offer some unique opportunity to study dispersal: their phenotype can be modified [61], they can be raised in laboratory [62], their population can be manipulated either in nature or in semi-natural conditions [63,64], and, most importantly, a large majority of the dispersal events can be recorded and dispersal is restricted to some given part of their life cycle [65]. Dispersal has been studied in detail in at least two species, the side-blotched lizard (*Uta stansburiana*) and the common lizard (*Zooteca vivipara*). In these two species, kin interactions have been demonstrated to shape dispersal pattern both for emigration and immigration [63,66-68]. It has also been showed that kin-based dispersal is phenotype dependent, and associated with multiple traits ranking from physiology through behaviors to life-history traits [61,67]. In the common lizard, kin-based dispersal is mediated by other cues than congener-based dispersal [69,70]. While kin-based dispersal is prenatally determined, congener-based dispersal is determined after birth. This clearly raises the question of whether dispersal is a single behavior or a collection of behaviors with the movement in response to alterations in the social or non-social environment as the only common part ([71,72] for a review). Many of these factors do not only influence emigration decisions but also immigration decisions, especially with respect to the social environment [73].

Lizards are ectotherms, i.e. their metabolism and activity are temperature-dependent. A suite of papers ([11,60,74]) demonstrated that the thermal niche is a key parameter to understand lizards response to climatic changes. In the common lizard, survival and fecundity are enhanced by a raise in temperature, as shown by two decades capture-mark recaptures surveys in six populations [75]. While these populations are situated on the warm margin of the distribution of the species, they were found to benefit from climate warming. There are several potential explanations for this intriguing result. The common lizard typically inhabits rather humid habitats such as peat bogs, marshes, heaths and humid meadows. All the populations studied were selected in such habitats, and not in drier habitats where populations are less dense. We have some evidences that in humid habitats, climate warming has not yet altered the level of humidity, while in drier habitats (the matrix) the level of humidity has dropped significantly [76]. The end result is that in high quality habitat (humid ones) climate warming has increased the net productivity (more food) and enlarged the activity season (more time), which in turn has increased feeding efficiency and hence individual growth, fecundity and survival. Interestingly, dispersal rates (emigration as well as immigration) negatively correlated with climate warming in at least one

of these populations [76,77]. This result fits quite well the climatic scenario described above: high quality habitats appear of even better quality with climate warming, while poor quality habitats display the opposite trend. On the short term, restricting dispersal from high quality habitat appears adaptive under this scenario, as populations in the matrix are badly affected by drying and should therefore die out rapidly [77]. A large survey of common lizard populations along the warm margin of the species' distribution (from Spain to Balkans) recorded numerous population extinctions, especially in dry habitats [74]. If on the short term, a reduced dispersal is adaptive, this is certainly not the case on the long term since, eventually, even high quality habitat will also be dry out by climate warming. Escaping from these habitats will then be impossible: the current decrease in dispersal will thus lead the population in an evolutionary trap.

How is this related to the movement ecology paradigm? Individual thermal capacities are heterogeneous in common lizard populations. Differences among individuals in black back patterns (melanin based) parallel a difference in their ability to convert light into heat. During climate warming, the proportion of individuals with reticulated back patterns (warming up less rapidly) increased with respect to individuals with linear back patterns (warming up more rapidly), either due to selection or to plasticity [77]. When compared to individuals with linear back pattern, reticulated individuals were found to have a higher growth rate and a higher fecundity, and a lower juvenile survival, i.e. a shorter generation time. They also dispersed much less than linear individuals. We tried to apply some of the elements of the movement ecology paradigm to understand how this reduced dispersal was achieved. The techniques available to follow individual movements were not applicable for this species (juveniles being very small and living in a very highly structured habitat), we evaluated the resistance to movement of different elements of the habitat, i.e. humidity, darkness and soil texture. We choose to measure experimentally the time needed by an individual in a poor environment to cross different types of transient environments in order to reach a better habitat offered at a distant to the resident one. Despite being in a poor habitat, reticulated individuals were more reluctant to engage movement within a transient dry, dark or with no soil texture habitat than linear individuals [78]. Dispersal, and hence movement *per se*, is clearly encapsulated in a large syndrome associating thermal physiology, life history strategy and environmental perception which are themselves under the influences of individual past history (including maternal and grand maternal effects, [26]). This makes difficult any generalization from one particular situation to the next and cannot be really captured by the MEP. Indeed, the overall life history and the idea that multiple traits involved in movement have multiple functions in addition to movement, like melanin based back patterns for converting light into heat for general metabolism and activity, cannot be easily captured by the MEP mainly because focusing on single species trajectories is traded against acquiring data on other parameters and/or developing elaborated experimental designs.

Towards the emergence of a dispersal evolutionary ecology paradigm?

Most dispersal studies ultimately aim at providing reliable predictions of dispersal rates and distances, which is an objective of prime importance for an accurate modelling of metapopulation dynamics. Two different routes to dispersal predictions are possible, the Eulerian and Lagrangian approach, respectively (e.g. [79,80]). The Eulerian approach emphasizes the population and involves recording the redistribution of individuals among local populations. The Lagrangian approach involves the characterization of the magnitude, speed and directionality of individual movements. Given its focus on the focal individual, its properties and influential factors, the MEP is solidly grounded in the Lagrangian approach.

The Eulerian approach

The Eulerian approach is classically based on the construction of dispersal kernels representing the density of probability that dispersing individuals move a certain distance. More or less sophisticated theoretical distributions are usually fitted to empirical data to allow the prediction of dispersal distances [81]. If the probability that dispersing individuals move a certain distance is logically decreasing with the distance, this approach fails to consider that the matrix matters [82], i.e. that the landscape composition (including both the environmental and social contexts) is able to modulate dispersal decisions and distances by modifying dispersal costs. The recent rise of landscape genetics [83,84] moved the goalposts by providing direct measures of effective dispersal events between local populations, i.e. by quantifying the number of individuals that immigrate in a given local population at the previous generation and by providing their population of origin. The end product of dispersal measures using landscape genetics is now a (usually asymmetric) matrix of dispersal probabilities between pairs of local populations within a metapopulation, which integrates the whole dispersal process, from emigration to the reproduction of dispersers in their arrival population. Besides, methods of landscape genetics provide an estimate of the effects of various landscape elements on dispersal. Such an Eulerian approach based on landscape genetics seems convenient for the predictions of dispersal when information on only to and fro events are required, for instance to build models of metapopulation dynamics with the caveat that

dispersal probabilities are susceptible to show considerable temporal variation according to social factors like kinship, sex-ratio or density (e.g. [85]). This latter point illustrates that dispersal predictions using an Eulerian approach can be substantially improved by considering the phenotypes of the dispersers and the causes that push them to disperse: theory indeed suggests that dispersal distances vary according to the spatial scales of the processes triggering dispersal decision, the dispersal cause and the disperser syndromes (Figure 3 redrawn from [26,27,35,86]).

The Lagrangian approach

The Lagrangian approach considers the trajectory of the focal individual, which is at the heart of the MEP. It required previously considerable investment in data collection, which is more and more facilitated by the automatic acquisition of spatial positions, sometimes coupled with captors informing the internal state of the individual. At first glance, the Lagrangian approach seems a powerful tool in modelling dispersal in metapopulations: by first simulating individual trajectories according to the social and spatial contexts and then integrating their net results, it should be possible to predict the dispersal rates between local populations (e.g. [87]). However, the practical implementation of this approach is most often severely complicated by the ignorance of the rules affecting the movement of dispersing individuals. Such rules result from the many processes affecting individual movements, which are included into the basic description of the MEP but are critically lacking in most empirical studies so far (e.g. [17-19], but see [22,88] presenting efforts to fill this gap). The first critical question is about how to best incorporate the motivation pushing individuals to stay or to go, which depends on their internal state, but also of the interactions with the past and present environments. The MEP certainly offers some possibilities but clearly its remains work to rend it operational on such integration. To circumvent this limitation, it is indeed possible to use the emigration rate from a given local population to calibrate the number of trajectories that will be simulated. The next difficulty will then be to select the length of the trajectory. As previously mentioned, different dispersal causes will entail different dispersal distances (Figure 3). If the information about dispersal cause are not available, another proxy like mean dispersal distance has to be used. Another concern is the proportion of virtual individuals moving in the matrix that has to be removed to simulate dispersal mortality. This parameter is extremely difficult to assess from field studies, which forces the use of another proxy like the difference between the emigration and the immigration rate in all the local populations. The navigation component is most often a black box: what is the perceptual range, i.e. the distance from which individuals

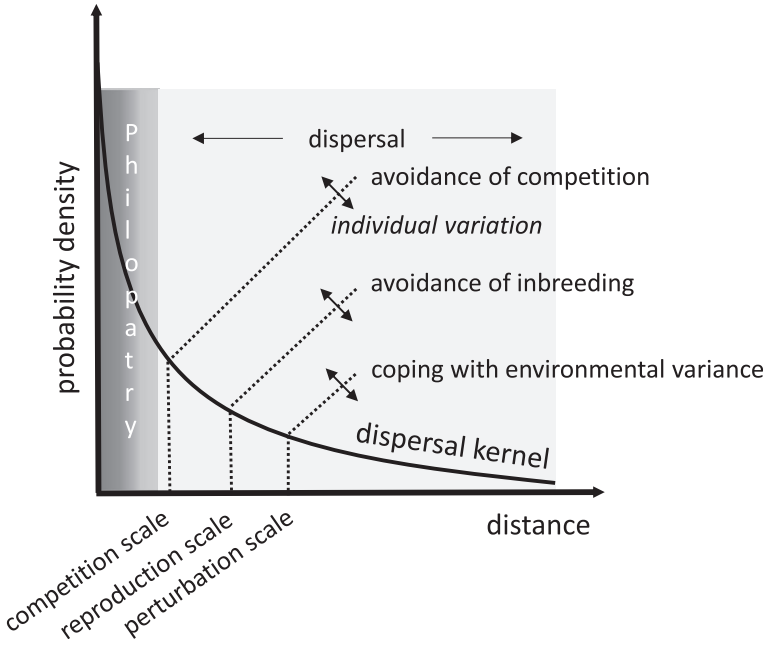

Figure 3 Hypothesized changes in dispersal distances according to different dispersal causes. Notice that the competition scale varies according to the relationship between the partners engaged in competition. Parent-offspring competition should entail short dispersal distances. Kin competition should generate variable dispersal distances according to the genetic structure of the population, eventually leading to colonization of new habitats by specially designed phenotypes. Conspecific competition should entail emigration out of populations. Modified from [18,26,27].

moving in the matrix will head towards a suitable habitat or an existing population? This parameter is here again most often missing in the behavioral literature. Finally, dispersal entails gene flow, i.e. the successful reproduction of immigrants in their arrival population. Only measures of effective dispersal assessed by genetic methods can provide such information, unless a direct count of immigrants and their offspring is possible, which is rarely the case.

Several attempts have been made to infer dispersal from individual trajectories using simpler models. Least cost path (LCP) models consider that dispersing individuals will react to the environmental context only, and that the trajectory of the individuals in a multi-element landscape will be constrained by the resistance of the landscape element to the movement of the disperser, which drives dispersal cost. The basic assumption of this method is that individuals will choose a trajectory that minimizes the cumulative costs of their displacement through the landscape. Reliable resistance estimate, i.e. costs of moving through a particular element can be effectively assessed by experiments [89] or by statistical inferences on real paths coupled to population genetic structure [90]. The corollary of this basic assumption is that dispersers have an innate, global knowledge of the landscape to navigate to neighbor populations by minimizing their travel costs in the matrix, which may be the case if optimal dispersal directions are selected over several generations or if they derived information from immigrants about the quality and location of their population of origin [91]. However, LCP models can be totally misleading if their basic assumption is not fulfilled: Stevens et al. [92] showed using landscape genetics that dispersing individuals in a complex landscape did not follow least cost paths at all but rather used the landscape element with the higher resistance to movement, which in fact provided food and shelter to the dispersing individuals. The stochastic movement simulator (SMS) developed by Palmer et al. [93]) is an alternative to the LCP. In essence, individuals moving through the landscape are able to choose their paths according to the landscape composition and their preferences for particular landscape element. They select their paths step by step using a limited perceptual range of the surrounding landscape elements. This procedure relaxes the critical assumption of LCP models that individuals have a total knowledge of their environment. Basically, SMS is much simpler than simulators based on movement rules inferred from real paths. But while applying SMS to real species on real landscapes is clearly possible and has potential advantages [94], it will often be a complex and challenging task, because it has to solve all the critical questions listed above about dispersal cause and propensity, dispersal syndromes, distance, mortality and perceptual range.

Combining the Eulerian and Lagrangian approaches

The two previous paragraphs illustrate that each approach has its advantages and shortcomings. The Eulerian approach inform on effective dispersal events (steps 1 and 3 of the dispersal process, Figure 4), which can then be related to the social and environmental contexts to identify which ecological and evolutionary processes drive are at work on dispersal. However, even if methods of landscape genetics assess the costs of dispersal among different landscape elements, the actual movement paths of dispersing individuals remain mostly unknown. The Lagrangian approach most often manages perfect descriptions of the topology of movement paths (step 2 of the dispersal process, Figure 4). However, its lacks the inclusion of biological processes that generate these movement paths, which therefore currently limits its predictive power. Combining the two approaches might be a good solution to improve the reliability of dispersal predictions for an accurate modeling of metapopulation dynamics. We propose thus a mixed approach where the Eulerian approach based on genetic data provides a backbone for the predictions of effective dispersal within a given metapopulation. We think that the Lagrangian approach could provide a high added value to this backbone by allowing simulating the effects of spatial and temporal variation in the social and environmental contexts. The number of movement rules that should be defined to let say determine the effects of changes in land cover or in inter-specific interactions will indeed be much lower to answer such targeted questions than to simulate the whole dispersal process. The resulting scenarios of changes in the between-population dispersal matrix could then be validated using landscape genetics. However, we acknowledge that in some cases (e.g. insect outbreaks) even the Eulerian approach could be useful to simulate the transience phase, which means that dispersal can then be modelled using simple dispersal kernels. We want thus to stress that the relative advantages of the Lagrangian/Eulerian approaches in capturing the dispersal process may be dependent both on the research questions and the study system.

Conclusions

Dispersal is a complex process given its variability and evolvability. We focused so far on the predictions of dispersal in metapopulations without referring that much to the four components of the MEP (internal state, external status, navigation, motion). To go further, we propose to combine our mixed Eulerian and Lagrangian approach with refined investigation of individual heterogeneity in dispersal phenotypes (Figure 4). The long term studies of dispersal in butterflies and lizards mentioned above indeed showed that the quality and the quantity of the current available data on these organisms are not detailed enough to

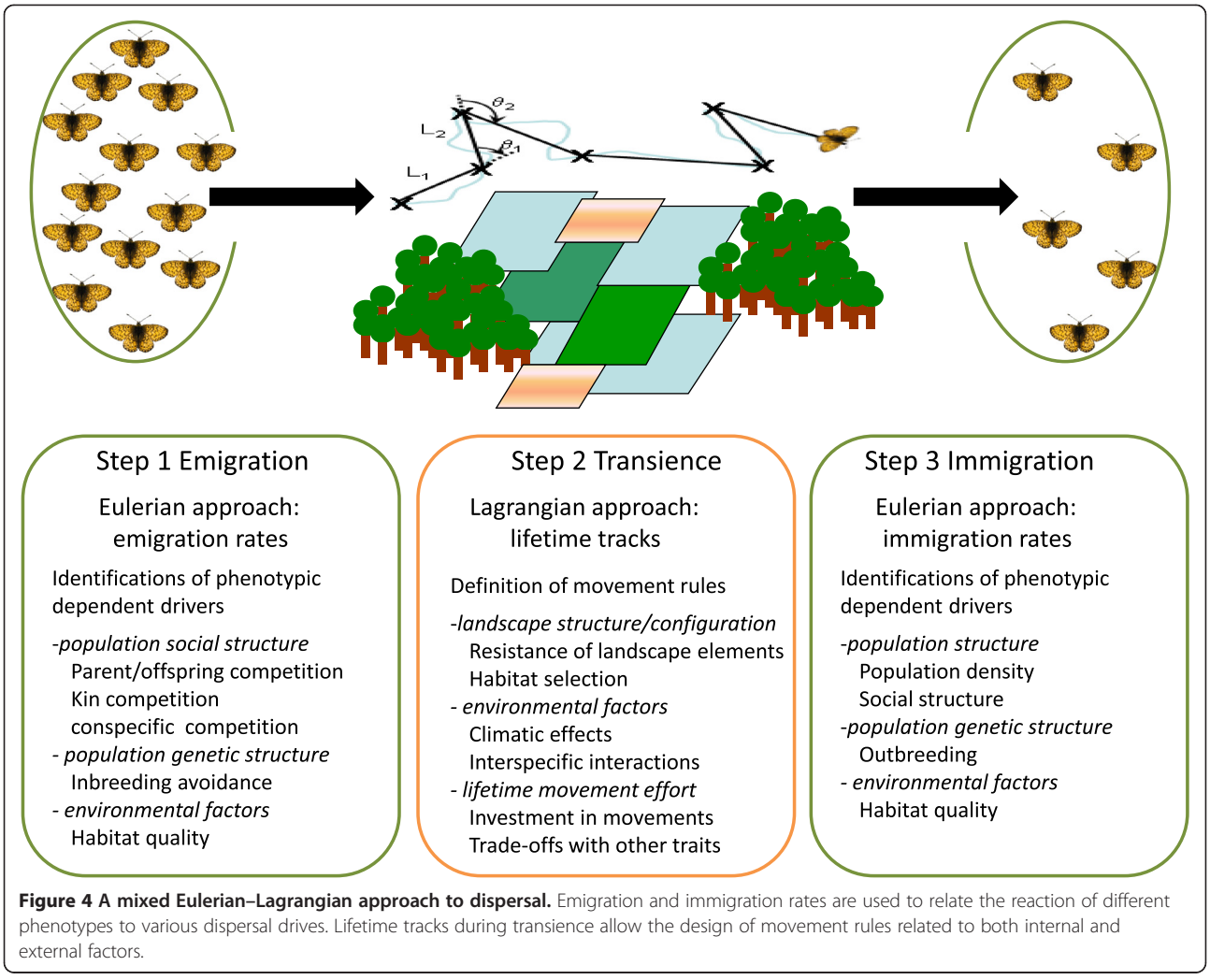

Figure 4 A mixed Eulerian–Lagrangian approach to dispersal. Emigration and immigration rates are used to relate the reaction of different phenotypes to various dispersal drives. Lifetime tracks during transience allow the design of movement rules related to both internal and external factors.

allow the implementation of the flow chart summarizing the MEP (Figure 1), even if the knowledge accumulated on the dispersal of these model organisms is preeminent in the field.

We believe that one major problem in the application of the MEP to dispersal is its current impossibility to relate the movement paths of an individual to its history and to their impact on fitness. Current empirical studies self-explicitly grounded in the MEP are focused towards the design of mechanistic models of movements. We think that the cleverest descriptions or predictions of individual tracks do not allow the identification of the biological processes that will influence the evolution of movements, preventing generalizations and emergence of a complete corpus of theory. We acknowledge that the founder paper of the MEP emphasized the importance of including key biological details in such models, even if there is track to practice. In our opinion, these three limitations (no link with fitness, no access to biological processes, no global theory) currently preclude the study of dispersal with the MEP as an unique framework. However, we think that the MEP might be central in dispersal studies, for instance by allowing the identification of the critical stages during which dispersal is shaped in the life cycle of an organism. The comparison of the variance of various movements (post-emancipation exploration, pre-migratory excursions, migration, winter foraging, etc.) with the variance of dispersal could help to understand which stage(s) of the life-cycle have critical influence on dispersal. This will provide the opportunity to make testable predictions on dispersal ontogeny.

Another issue could be to link lifetime tracks to life histories, both among and within species, to assess whether and how movements are inter-related with particular values of fitness-related traits. The key idea would be to put movement ecology in the context of life history trade-offs, for example by including a term describing movement types in the individual fitness. We thus introduce a new fitness dimension that we tentatively call *lifetime movement effort*. Using this dimension, it should then be possible

to identify trade-offs among different movements types and relative investments in the other fitness components (growth, sexual maturity, fecundity and survival), which should correspond to different dispersal strategies, and hence shape contrasted dispersal syndromes. We suggest to use lifetime energetic, i.e. how individuals acquire and manage their energy all over their life, as currency to assess how lifetime movement efforts are traded off against the other fitness components (see e.g. [95] for a framework on the use of energetics in the study of animal movements).

We want to highlight recent advances in modeling that have been made on coupling movement models to populations dynamics, including, in a small number of cases, evolution of the rules governing movement. This is an area where there has already been some coming together of the fields. There is a call coming from the MEP side for movement models to be integrated within models for spatial population dynamics [96,97]. From the eco-evolutionary dispersal side, there has been progress towards including movement rules and the evolution of those rules rather than just focusing on emigration decisions [98,99].

Finally, we think that the confrontation of the genetic profiles of different dispersal phenotypes, and of their variation of gene sequence and expression under contrasted social and environmental contexts is a promising avenue to solve the major black boxes that are currently associated with the application of the MEP to study dispersal. Candidate gene and mapping gene networks approaches are elegant ways of exploring the mechanisms of phenotypic evolution and adaptation to such changes in both contexts. By targeting candidate genes related to dispersal and unraveling the genetic architecture of dispersal syndromes, including motion and navigation capacities, we can gain key insights into the regulatory changes that may allow individuals, and hence populations to respond to changes in social or environmental contexts. Candidate genes approaches could be involved either in shaping behavioral syndromes like "Drd4", the dopamine receptor D4 gene in vertebrates [100,101], or "Foraging" that encodes a cGMP activated protein kinase in insects [102,103] or metabolic pathways important for locomotion like "pgi" coding for phosphoglucose isomerase, a metabolic enzyme important in supplying energy to the flight muscles in insects [104]. Examining genome-wide regulatory changes would be excellent to unravel the genetic architecture of dispersal syndromes as even small differences in gene expression can be detected across the entire genome. Variation in gene expression levels could provide important insights not only on the motion and the navigation capacities of different dispersal phenotypes, but also on changes in the internal state of the individuals under changing conditions (i.e. phenotypic plasticity), which is the most important challenge in applying the MEP to the study of dispersal. Overall, the adoption of such an integrative approach linking the study of gene variation and expression to condition- and phenotypic-variation in dispersal will certainly provide a breakthrough in dispersal research and possibly the emergence of a real dispersal evolutionary ecology paradigm on the model of the MEP.

Competing interests
The authors declare that they have no competing interests.

Authors' contribution
All authors discussed the content of the paper. MB and JC wrote a first draft, which was commented by all authors. All authors read and approved the final manuscript.

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